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Phylogenetic analysis of species of the neotropical social wasp *Epipona* Latreille, 1802 (Hymenoptera, Vespidae, Polistinae, Epiponini)

Sergio R. Andena[1], James M. Carpenter[2], Kurt M. Pickett[1]

1 *University of Vermont – Department of Biology, Marsh Life Science Building, 109 Carrigan Drive, Burlington, Vermont 05405, USA* **2** *Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA*

Corresponding author: *Sergio R. Andena* (sergioricardoandena@gmail.com)

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Abstract

The Neotropical social wasp genus *Epipona* is reviewed. Phylogenetic analysis of the species in the genus using morphological and nest characters resulted in a single cladogram, with the following ingroup topology: (*E. guerini* + *E. niger*) + (*E. media* + (*E. quadrituberculata* + *E. tatua*)). A key to the five species is presented.

Keywords

Paper wasps, cladistics, Vespidae, Epiponini

Introduction

Epipona is a neotropical genus of social wasps with five described species: *Epipona guerini* (de Saussure, 1854), *E. media* Cooper, 2002, *E. niger* (Brèthes, 1926), *E. quadrituberculata* (Gribodo, 1892) and *E. tatua* (Cuvier, 1797). Their distribution extends from Mexico to Bolivia (Cooper 2002). The genus is diagnosed by the presence of a shining black cuticle and a bidentate clypeus (Carpenter 2004). The nests of *Epipona* are arboreal, usually found high in trees, and have a sessile initiation (Wenzel 1998). The nests are constructed of a dense, brittle carton that is composed of short chips of gray or brown coarse matter. There are multiple combs that are sessile on the envelope

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of the preceding comb. The envelope is asymmetrical with a small exit hole opposite the lower side of a flat or slightly concave bottom.

Caste dimorphism has been studied in two species of *Epipona*: *E. tatua* (Richards 1978; Noll and Wenzel 2008) and *E. guerini* (Hunt et al. 1996). In these species, the queens are larger than the workers. Although the remaining three species have not been studied in this regard, *Epipona* is nested within a clade in which egg laying females are larger than non-egg layers in nearly all measurements (Noll and Wenzel 2008), and so this is probably characteristic of the genus.

As *Epipona* has a complex taxonomic history (see below) including misidentification of species, we present a revised identification key to the species in addition to a phylogenetic analysis.

Taxonomic background

The genus *Epipona* was described by Latreille (1802) for two species: *Vespa nidulans* Fabricius, 1793 [= *Vespa artifex* Christ, 1791] and *Vespa tatua* Cuvier, 1797 [= *Vespa morio* Fabricius, 1798, synonymized by White (1841: 316)]. Blanchard (1840: 394) designated *Epipona morio* as the type of the genus. De Saussure (1854) proposed the name *Tatua* as a substitute for *Epipona* Latreille, under the erroneous impression that Latreille had previously used the name for another group of wasps in the Eumeninae. De Saussure (1854) included *Tatua morio* and the new species *Tatua guerini* de Saussure in the genus. Gribodo (1892) described the new species *Tatua quadrituberculata.* Ducke (1910: 489) recognized only one species, *Tatua tatua,* synonymizing *T. guerini* and *T. quadrituberculata.* Brèthes (1926) described the species *niger* in the genus *Coloboclypeus*. Bequaert (1938) concluded that *T. guerini* was structurally different from *T. tatua,* restoring it to species status.

Richards (1978), who had not seen the types of *quadrituberculata* and *guerini*, recognized three species in the genus: *Epipona guerini, E. tatua* and *E. quadrituberculata.* He synonymized *C. niger* Brèthes with *E. guerini*. Carpenter (1999) examined the types of *E. guerini* and *E. quadrituberculata* and pointed out that *E. quadrituberculata sensu* Richards was a misidentification of *E. guerini* (de Saussure), while *E. quadrituberculata* (Gribodo) was another species, not recognized by Richards. Carpenter (1999) also pointed out that the correct name for *E. guerini sensu* Richards was *E. niger* (Brèthes). Cooper (2002) examined some of the specimens of *E. quadrituberculata* determined by Richards, and described for them a new species, *E. media.*

In Carpenter's (1991) phylogeny of the genera of Polistinae, *Epipona* was a member of a clade that he termed the *Epipona-Occipitalia* component. *Epipona* was sister to all other members of this clade, which included *Synoeca*, *Clypearia*, *Asteloeca*, *Metapolybia*, and *Occipitalia* (later synonymized with *Clypearia* by Carpenter et al. 1996). Wenzel (1993), using nest characters, found a sister-group relationship between *Epipona* and *Synoecoides* (later synonymized with *Polybia* by Carpenter et al. 2000). Wenzel and Carpenter (1994), combining morphological, nest architecture and larval characters

also placed *Epipona* as sister group of *Synoecoides* (=*Polybia*). Noll et al. (2004) included discretized morphometric measurements of caste differentiation in the matrix of Wenzel and Carpenter (1994), and found a sister-group relationship between *Epipona* and *Polybia*, which is consistent with the findings of Wenzel and Carpenter (1994). Arévalo et al. (2004) presented an analysis of combined molecular and morphological/behavioral data, and placed their exemplar of *Epipona* in an unresolved trichotomy with *Metapolybia* and *Synoeca*, a result more consistent with Carpenter (1991).

Materials and methods

Specimens were examined in the American Museum of Natural History (AMNH) and in the University of Vermont, and borrowed from the Bohart Museum of Entomology, USA (UCDC); Cornell University, USA (CUIC); the Field Museum of Natural History, USA (FMNH); the Museo Civico di Storia Naturale "Giacomo Doria," Italy (MSNG); the Muséum National d'Histoire Naturelle, France (MNHN); the Museum of Zoology, University of Michigan, USA (UMMZ); and the Snow Entomological Museum, University of Kansas, USA (SEMC). A complete list of specimens studied can be found in Appendix 1. The characters and their respective states are listed in Table 1, and partially illustrated in figures 1–12. Thirty female morphological characters and 12 nest characters were assembled in a data matrix for phylogenetic analysis (Table 2).

Table 1. Character list for *Epipona*.

Character	States
1	*Cuticle:* opaque, maculate = 0; shining, black = 1.
2	*Shape of clypeus:* wider than long = 0; as long as wide = 1; longer than wide = 2.
3	*Apex of clypeus:* sharply pointed = 0; rounded = 1; truncate = 2; weakly bidentate = 3.
4	*Clypeal lateral lobes:* well developed = 0; reduced and rounded = 1.
5	*Ocellar distance:* separated by about an ocellar diameter = 0; separated by more than one ocellar diameter = 1.
6	*Hairs on frons and vertex:* short and sparse = 0; long and dense = 1; absent = 2.
7	*Macropunctures on frons and vertex:* absent, micropunctures only = 0; scattered, medium punctures = 1; coarse and dense = 2; shallow and very sparse = 3.
8	*Gena:* more than half width of eyes = 0; less than half width of eyes = 1.
9	*Vertex:* posteriorly concave = 0 (Fig. 10); markedly excavated posteriorly = 1 (Fig. 9).
10	*Occipital carina:* present = 0; absent = 1.
11	*Pronotal dorsal carina:* present = 0; absent = 1.
12	*Humeri:* rounded = 0; slightly produced = 1 (Fig. 1); strongly produced = 2.
13	*Pronotal fovea:* present = 0; absent = 1.
14	*Pretegular carina:* present = 0; absent = 1.
15	*Macropunctures on pronotum:* absent = 0; dense dorsally, becoming sparser ventrally = 1; coarse, dense throughout = 2; sparse and very fine = 3; superficial throughout = 4; medium throughout = 5.

Character	States
16	*Dorsal groove:* present = 0; absent = 1.
17	*Macropunctures on scutum and scutellum:* absent = 0; dense, medium = 1; dense, coarse = 2; scattered, fine = 3; very sparse, fine = 4; dense, fine = 5.
18	*Median scutellar line:* shallowly impressed = 0; markedly depressed behind = 1; absent or evanescent = 2; evanescent behind = 3.
19	*Metanotum:* rounded = 0; compressed = 1.
20	*Metanotal tubercle:* absent = 0; present = 1.
21	*Macropunctures on metapleuron:* absent or evanescent = 0; scattered medium puctures present throughout = 1; scattered fine punctures present throughout = 2; coarse = 3; few dorsal punctures = 4.
22	*Propodeal concavity:* narrow = 0; shallow, broad = 1; posterior only, deep = 2; narrow, deep = 3; very broad, shallow = 4; narrow, ventrally deep, propodeum forming large lateral lobes = 5; with a slight concavity above propodeal orifice = 6.
23	*Propodeal concavity sculpture:* smooth = 0; with scattered dense punctures = 1; with coarse punctures and lateral carinae = 2 (Fig. 4); rugose with transverse carinae = 3 (Fig. 3); densely reticulate, fine punctures = 4; with large, dense punctures = 5.
24	*Propodeal orifice:* longer than wide = 0; as wide as long = 1.
25	*First metasomal segment:* petiolate, longer than wide = 0; filiform, short, dilated at sides = 1; filiform, long, not dilated at sides = 2; filiform basally, widening abruptly after spracles = 3; wide, much wider than long = 4; narrow, wider than long = 5; petiolate, transversely widened posteriorly = 6.
26	*Anterior third of pre-spiracular area of Tergum I:* convex above = 0 (Figs 5 and 6); flat above = 1.
27	*Tergum I basal projections:* absent = 0; present = 1 (Fig. 5).
28	*Hairs on Tergum I:* outstanding hairs sparse = 0 (Fig. 6); outstanding hairs very long and dense = 1 (Fig. 5); short, dense pile = 2.
29	*Tergum II sculpture:* macropunctures absent = 0; shining with shallow punctures = 1; shining with dense, coarse punctures = 2; reticulate-coriaceus, with moderate punctures = 3 (Fig. 11); reticulate-coriaceus, with very sparse, fine punctures = 4 (Fig. 12); reticulate-coriaceus, with dense and fine punctures = 5.
30	*Vand der Vecht's gland:* external modified area present = 0; externally absent = 1.
31	*Comb pedicel:* rodlike pedicel present = 0; absent = 1.
32	*Comb foundation:* without foundation of pulp = 0; with foundation of pulp = 1.
33	*Comb number:* multiple = 0; single = 1.
34	*Comb expansion:* gradual = 0; absent = 1; contiguous blocks = 2; rapid construction of several layers = 2.
35	*Envelope shape:* flask shaped = 0; dome shaped = 1.
36	*Envelope entrance:* long, downward spout = 0; short, peripheral collar = 1; simple hole = 2.
37	*Envelope entrance placement:* ventral = 0; dorsal or lateral = 1.
38	*Bottom of nest:* convex = 0; flat, asymmetrical = 1.
39	*Secondary envelopes:* secondary combs without envelopes = 0; secondary combs with envelopes = 1.
40	*Envelope expansion:* remodeled to allow comb to grow beyond initial periphery = 0; prefabricated, restricting comb growth to initial diameter = 1
41	*Material:* coarse long fiber = 0; coarse chips = 1
42	*Carton:* supple = 0; brittle = 1; dense, white = 2; dense, brown or gray = 3.

Table 2. Character matrix for *Epipona*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Angiopolybia pallens	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudopolybia difficilis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Synoeca cyanea	0	0	1	1	0	2	3	0	0	1	1	0	1	0	3	1	4	0	0	0	0	6	1	0	3	0	0	2	0	1	1	0	0	0	1	1	0	0	0	0	1	1
Protopolybia bituberculata	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	0
Charterginus xanthura	0	2	2	1	1	1	2	1	0	0	0	1	0	1	2	1	2	0	1	1	3	5	5	0	6	0	0	0	2	1	1	1	1	1	1	2	1	0	0	0	0	1
Chartergus artifex	0	0	1	1	1	0	1	0	0	0	0	2	1	0	1	1	1	0	1	1	4	4	1	0	4	0	0	0	1	1	1	1	0	2	1	2	0	0	1	1	0	2
Protonectarina sylveirae	0	0	1	1	1	1	3	0	0	0	0	1	0	0	4	1	5	0	0	0	0	3	1	0	5	0	0	0	1	1	1	1	0	2	1	2	0	0	1	1	0	0
Polybia jurinei	0	1	1	1	0	0	1	0	0	0	0	0	0	0	5	1	5	3	0	0	2	1	1	0	0	0	0	0	0	1	1	1	0	2	1	2	0	0	1	1	1	1
Epipona guerini	1	0	3	1	0	2	1	0	0	1	1	0	1	0	1	1	3	0	0	0	4	2	3	1	2	1	0	0	4	1	1	1	0	2	1	2	0	1	1	1	1	3
Epipona media	1	0	3	1	0	2	1	0	0	1	1	0	1	0	1	1	3	1	0	0	1	2	2	1	2	0	0	0	4,5	1	1	1	0	2	1	2	0	1	1	1	1	3
Epipona niger	1	0	3	1	0	2	1	0	1	1	1	0,1	1	0	1	1	3	0	0	0	0	2	3	1	2	1	0	0	4	1	1	1	0	2	1	2	0	1	1	1	1	3
Epipona quadrituberculata	1	0	3	1	0	2	1	0	0	1	1	1	1	0	1	1	3	1	0	0	1	2	2	1	1	0	1	1	3	1	1	1	0	2	1	2	0	1	1	1	1	3
Epipona tatua	1	0	3	1	0	2	1	0	0	1	1	0,1	1	0	1	1	3	1	0	0	1	2	2	1	1	0	0	0	3	1	1	1	0	2	1	2	0	1	1	1	1	3

The analysis was undertaken using the program TNT (Tree analysis using New Technology; Goloboff et al. 2008). Multistate characters were treated as non-additive (Fitch 1971), with the exception of character 12, which was treated as additive (Farris 1970). The following outgroups were used to test the monophyly of *Epipona*: *Angiopolybia pallens, Pseudopolybia difficilis, Synoeca cyanea, Protopolybia bituberculata, Charterginus xanthura, Chartergus artifex, Protonectarina sylveirae* and *Polybia jurinei*. The tree was rooted to *Angiopolybia pallens*.

Results

Analysis of the matrix by implicit enumeration resulted in a single cladogram of length 102, consistency index 0.82 and retention index 0.82 (Fig. 13). The species of *Epipona* are supported as a monophyletic group, with the following relationships among them: (*E.guerini* + *E. niger*) + (*E. media* + (*E. quadrituberculata* + *E. tatua*)). This cladogram also resulted from implied weighting (default concavity).

Discussion

Compared to previous cladograms of the Epiponini (Carpenter 1991; Wenzel 1993; Wenzel and Carpenter 1994; Noll et al. 2004), the relationships of the genera are somewhat different (see above). Here *Epipona* is the sister-group of *Synoeca.* As this is a treatment of *Epipona*, and not of the outgroups, we defer to these previous works for the relationships among the genera.

In our hypothesis of phylogenetic relationships *Epipona* is a monophyletic genus, supported by the following synapomorphies: the cuticle shining and black [character 1 (state 1)], the clypeus weakly bidentate [ch. 3 (3)], the propodeal orifice as wide as long [ch. 24 (1)], Tergum II reticulate-coriaceus with very sparse and fine punctures [ch. 29 (4)]; the bottom of the nest flat and asymmetrical [ch. 38 (1)] and the nest carton dense, brown or gray [ch. 42 (3)]. The macropunctures on the scutum and scutellum scattered and fine [ch. 17 (3)] and the propodeal concavity posterior only and deep [ch. 22 (2)] are also features shared only by the species of *Epipona,* but these characters are ambiguously optimized on Fig. 13, with the ancestral states being unclear, and hence are not plotted.

Richards (1978: 158) cited all these features in diagnosing *Epipona*, except the macropunctures on the scutum and scutellum. In addition, he cited the pronotum without a fovea, also discussed in Carpenter (1991), which is shared with many other genera and, probably, had independent losses within Epiponini; the propodeum with a more or less deep and rounded concavity, being coarsely sculptured, punctate or keeled (= carinate) or both (Figs 3 and 4); and Tergum I forming a somewhat broad and flattened petiole, with the rest of the gaster being cordiform, widening suddenly after Tergum I (Figs 5 and 6). As these last two features were erroneously described by

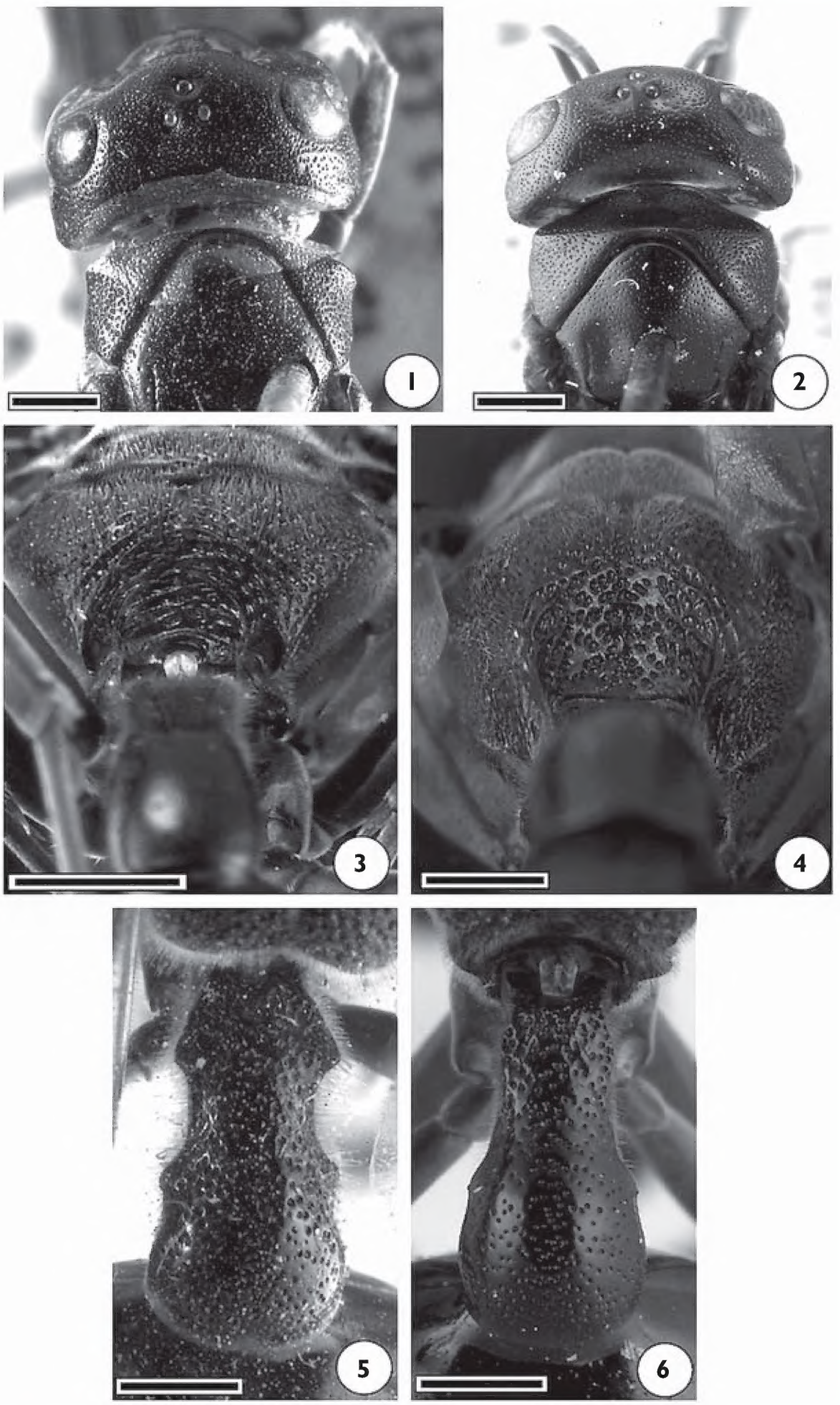
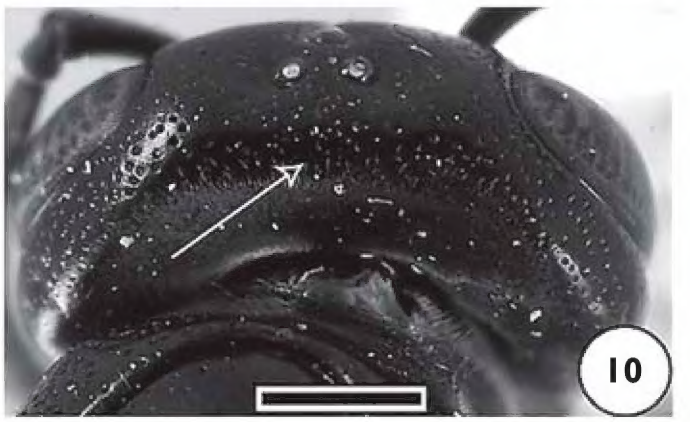
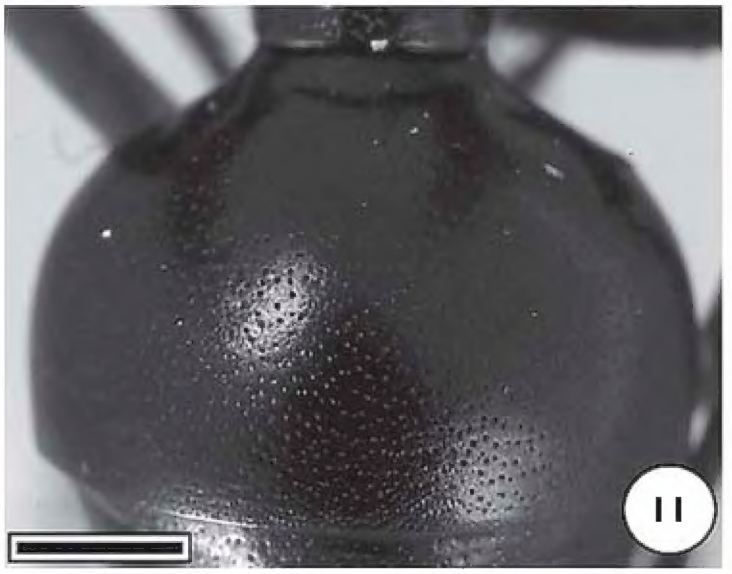


Figure 1. *E. quadrituberculata*, humeri, dorsal view. Scale bar = 1.0 mm.
Figure 2. *E. tatua*, humeri, dorsal view. Scale bar = 1.0 mm.
Figure 3. *E. guerini*, propodeal concavity, frontal view. Scale bar = 1.0 mm.
Figure 4. *E. tatua*, propodeal cancavity, frontal view. Scale bar = 1.0 mm.
Figure 5. *E. quadrituberculata*, Tergum I, dorsal view. Scale bar = 1.0 mm.
Figure 6. *E. tatua*, Tergum I, dorsal view. Scale bar = 1.0 mm.





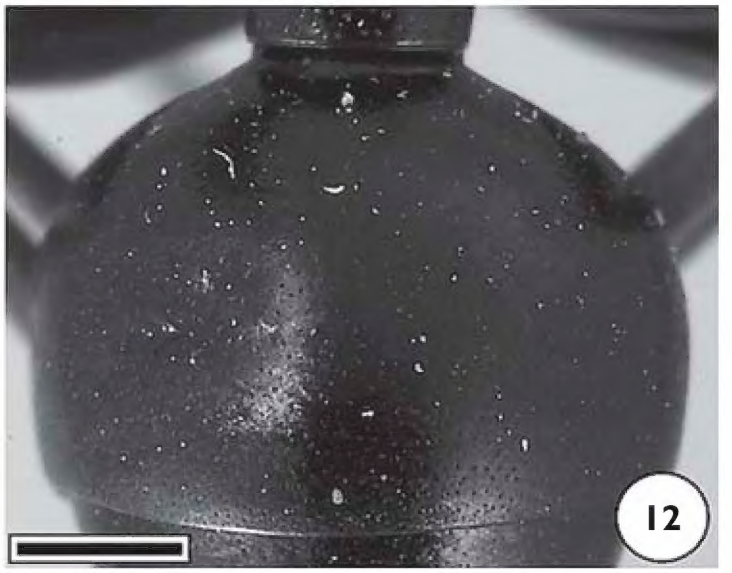


Figure 8. *E. niger*, propodeum, dorsal view. Scale bar = 1.0 mm.
Figure 9. *E. guerini*, propodeum, dorsal view. Scale bar = 1.0 mm.
Figure 10. *E. niger,* head, dorsal view. Scale bar = 1.0 mm.
Figure 11. *E. guerini,* head, dorsal view. Scale bar = 1.0 mm.
Figure 12. *E. tatua*, Tergum II, dorsal view. Scale bar = 1.0 mm.
Figure 13. *E. media*, Tergum II, dorsal view. Scale bar = 1.0 mm.

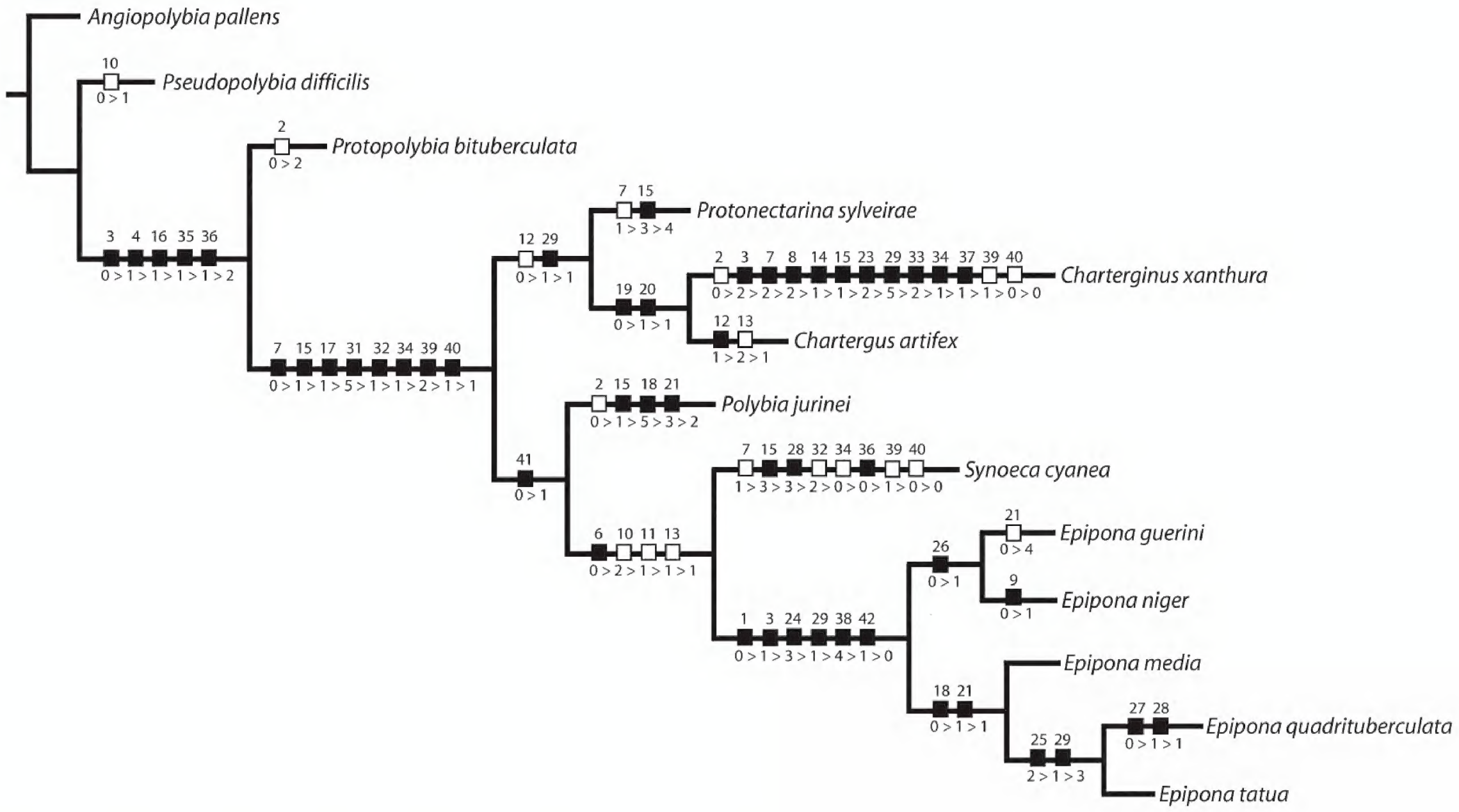

Angiopolybia pallens
10
0 > 1
Pseudopolybia difficilis
2
0 > 2
Protopolybia bituberculata
3 4 16 35 36
0 > 1 > 1 > 1 > 1 > 2
7 15
1 > 3 > 4
Protonectarina sylveirae
12 29
0 > 1 > 1
2 3 7 8 14 15 23 29 33 34 37 39 40
0 > 2 > 2 > 2 > 1 > 1 > 2 > 5 > 2 > 1 > 1 > 1 > 0 > 0
Charterginus xanthura
19 20
0 > 1 > 1
12 13
1 > 2 > 1
Chartergus artifex
7 15 17 31 32 34 39 40
0 > 1 > 1 > 5 > 1 > 1 > 2 > 1 > 1
2 15 18 21
0 > 1 > 5 > 3 > 2
Polybia jurinei
41
0 > 1
7 15 28 32 34 36 39 40
1 > 3 > 3 > 2 > 0 > 0 > 1 > 0 > 0
Synoeca cyanea
6 10 11 13
0 > 2 > 1 > 1 > 1
21
0 > 4
Epipona guerini
26
0 > 1
9
0 > 1
Epipona niger
1 3 24 29 38 42
0 > 1 > 3 > 1 > 4 > 1 > 0
Epipona media
18 21
0 > 1 > 1
27 28
0 > 1 > 1
Epipona quadrituberculata
25 29
2 > 1 > 3
Epipona tatua

Figure 13. Cladogram of species of *Epipona*. Character numbers (see table 1) are placed above hash marks, with the state numbers below, separated by ">" to indicate the transitions between states. Filled hash marks indicate an uncontroverted step, while open hash marks indicate homoplastic change.

Richards (1978), they presumably were crucial in the misidentification by Richards (1978) of the species of *E. guerini, E. niger* and *E. quadrituberculata*. These features must be better understood (see below).

Based on those two features the species of *Epipona* might be divided into two groups: (1) *E. guerini* + *E. niger* and (2) *E. media* + (*E. quadrituberculata* + *E. tatua*). The propodeal concavity of group 1 always shows transverse carina, or it is rugose (Fig. 3) *versus* coarsely punctate in group 2 (Fig. 4). Cooper (2002) observed carinae more irregular in some Venezuelan specimens of *E. niger,* while *E. guerini* has a more rugose concavity. Cooper (2002) also mentioned that for some Mexican specimens of *E. guerini* the concavity is more carinate, which was also observed by us not only in Mexican but also in Costa Rican specimens. Specimens of *E. niger* from Panama and Costa Rica (see Appendix 1) show a stronger longitudinal carina on the propodeal concavity, the punctation on the propodeum denser and the vertex less excavated posteriorly than specimens from South America. For *E. tatua* Richards (1978: 159) stated that very rarely there are a few striae on the posterior face of the propodeum, but in fact, these striae (=carinae) are present not only in *E. tatua,* but in *E. quadrituberculata* and *E. media* as well.

The distribution of *E. guerini* has been reported from Mexico to Costa Rica (Cooper 2002), however one specimen studied in this work is from Panama [Boquete (UMMZ), see Appendix 1]. Boquete is a town located in the northern region of Panama, about 40 km (in straight line) from the Costa Rican border, so the finding of *E. guerini* in this location is unsurprising.

Cooper (2002) observed that only *E. guerini* and *E. niger* have the anterior third of Tergum I flattened, thus being synapomorphic for this clade in our cladogram [ch. 26 (1)]. The specimens of *E. media* studied here have the anterior third of Tergum I slightly compressed, which may be another transitional state between *E. guerini* + *E. niger* and *E. quadrituberculata* + *E. tatua* (see below).

According to Cooper (2002: Figs 6 and 7) *E. niger* has the humeri more produced and acute than *E. guerini,* but we have seen variation in this character for *E. niger*, and so it is polymorphic in our matrix. Specimens of *E. niger* from Colombia, Ecuador and Peru usually have the humeri more produced, but not all.

Richards (1978), in his key, cited hairs short and not numerous in *E. quadrituberculata* and numerous outstanding hairs in *E. guerini,* but as already noted above, he had misidentified these species. Cooper (2002: Figs 10 and 11) depicted sparse and short hairs for *E. tatua*, and denser, numerous hairs in *E. quadrituberculata* (see also Figs 5 and 6). Specimens of *E. guerini* from Costa Rica have the density of hairs like *E. tatua,* with them less abundant in *E. media* and *E. niger,* however some specimens of *E. tatua* from Peru and Brazil have the density of hairs nearly as in *E. quadrituberculata*; but in these four species the hairs are shorter than in *E. quadrituberculata.* Carpenter (1999) also cited hairs denser for *E. quadrituberculata* and, as depicted in Fig. 5, they are also longer.

The clade *E. media* + (*E. quadrituberculata* + *E. tatua*) is supported by the medial scutellar line markdely depressed behind [ch. 18 (1)] and the metapleuron with medium macropunctures throughout [ch. 21 (1)], also cited by Cooper (2002). *Epipona guerini* has the metapleuron more opaque and with fine and very sparse punctures

dorsally. In Richards's (1978) key, *E. guerini* is described as unpunctured on the metapleuron, but this means *E. niger*, which has no punctures on the metapleuron and is unique in *Epipona* (see also Cooper 2002). *Epipona media* has the metapleuron slightly opaque, densely punctate throughout, and the humerus slightly produced. As this species share features of both clades, *E. guerini* + *E. niger* and *E. quadrituberculata* + *E. tatua,* its position is well established as intermediate.

Finally the clade *E. quadrituberculata* + *E. tatua* is supported by the first metasomal segment dilated at sides [ch. 25 (1)] and Tergum II coriaceus with moderate punctures [ch. 29 (3)]. Some specimens of *E. tatua* from Peru (San Martin and Ucayali River, see list of species) and Brazil (Porto Velho) have the humeri produced like *E. quadrituberculata,* and so it is polymorphic for this character (Figs 1 and 2).

Despite the complicated taxonomic history for these two species; they can be easily separated by the remarkable Tergum I, which is strongly produced and acute laterally in *E. quadrituberculata* (Fig. 5) *versus* less produced and rounded in *E. tatua* (Fig. 6). As Carpenter (1999: 9) mentioned "'Although still only known from one specimen, *quadrituberculata* seems more likely to be a species than a teratology," which was confirmed by Cooper's (2002) report of two specimens from the same region that agreed well with the diagnosis of this species.

Identification key for the species of *Epipona*

The identification key presented here is a revision of Cooper's (2002) key, to include only characters of females, which were also used in the phylogenetic analysis.

1 Propodeal concavity with transverse carinae or rugae reaching middle (Fig. 3); medial scutellar line shallowly impressed; metapleuron impunctate or with fine and sparse punctures on upper region; Tergum I with anterior third of pre-spiracular area flat above; Tergum II coriaceous, without obvious punctation or with shallow and very sparse punctation **2**

1' Propodeal concavity coarsely punctate, without transverse carinae or rugae present only at edge of lateral region, absent medially (Fig. 4); median scutellar line markedly depressed behind; metapleuron punctate ventrally; Tergum I with anterior third of pre-spiracular area convex above; Tergum II usually punctate..... **3**

2 Vertex strongly excavated posteriorly (Fig. 9); propodeal punctation medium to dense, usually with conspicuous, impunctate anterodorsal area (Fig. 7) .... ***E. niger*** **(Brèthes)**

2' Vertex only concave posteriorly (Fig. 10); propodeal punctation dense, punctate throughtout (Fig. 8) ..... ***E. guerini*** **(de Saussure)**

3 Tergum I with wide lateral projections anteriorly, with very dense, long hairs (Fig. 5); pronotum markedly projecting at humerus (Fig. 1); Tergum II with punctation evident..... ***E. quadrituberculata*** **(Gribodo)**

3' Tergum I without lateral projections anteriorly, with sparse to medium hairs (Fig. 6); pronotum not or slightly projecting at humerus (Fig. 2); Tergum II with or without evident punctation **4**

4 Tergum II shining or sometimes slightly coriaceous with numerous moderate punctures (Fig. 11) ..... ***E. tatua* (Cuvier)**

4' Tergum II opaque to slightly shining, coriaceous with punctures fine and sparse, sometimes not evident (Fig. 12)..... ***E. media* Cooper**

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Appendix 1 – Localities for specimens studied.

Epipona guerini: **Costa Rica** [Cartago, 3♀ (SEMC); Guanacaste, Estac. Mongo, SW Volcán Cacao, 1♀ (AMNH); Guanacaste, Volcan Orosi, 1♀ (AMNH); Heredia Prov., 1♀ (SEMC); Heredia, Vara Blanca, Finca Georgina, 1♀ (AMNH); Monte Redunda, 1♀ (UCDC); Rio Chitaria 1♀ (UCDC); San Jose, 2♀ (UCDC), 5♀ (AMNH), 6♀ (SEMC); San Jose, San Antonio de Escazu, 1♀ (AMNH); Tres Rios, 4♀ (CUIC); locality not specified, 1♀ (MNHN)]; **Guatemala** [Chichicastenargo, 1♀ (AMNH); Coban, 1♀ (AMNH); Guatemala City, 1♀ (UCDC); Paizum, 8♀ (CUIC); Panajachel, 6♀ (UCDC); Santa Catarina Pinula, 1♀ (UCDC); Zacapa Albores, 1♀ (UCDC); Yepocapa, 2♀ (FMNH); locality not specified, 2♀ (MNHN)]; **Honduras** [San Marcos, 1♀ (CUIC); Tela, 3♀ (UMMZ); locality not specified, 3♀ (AMNH)]; **Mexico** [Acayucan, 2♀ (UCDC); Cintalapa, 1♀ (UCDC); Chiapas, 1♀ (SEMC), 1♀ (UCDC); Cordoba, 4♀ (UCDC); Fortin de las Flores, 2♀ (UCDC); Ixtapa, 4♀ (UCDC); Jalapa, 1♀ (UCDC); Orizaba, 3♀ (MNHN), 3♀ (UCDC); San Cristobal, 4♀ (CUIC); Teziutlan Pueblo, 1♀ (SEMC); Teopisca, 5♀ (UCDC); Puebla, 1♀ (SEMC); Vera Cruz, 1♀ (SEMC), 7♀ (UCDC)]; **Panama** [Boquete, 1♀ (UMMZ)].

Epipona media: **Bolivia** [Chimore, 1♀ [paratype] (AMNH); Chimore Locotal, 1♀ [paratype] (AMNH)]; **Brazil** [Jaravi River, Estirão do Equador, 1♀ [paratype] (AMNH); Napo [paratype] (MNHN); Pará State, locality not specified, 2♀ (CUIC)]; **Colombia** [Putumayo, Mocoa, 1♀ (AMNH)]; **Peru** [Madre de Dios, Avispas, 1♀ [paratype] (AMNH); Tingo Maria, 1♀ [paratype] (AMNH)].

Epipona niger: **Colombia** [Antioquia-Guarne, 2♀ (SEMC); Antioquia, Rio Porce, 1♀ (SEMC); Bogotá, 2♀ (MNHN); Magdalena, 1♀ (AMNH); Rio Anchicaya, 2♀ (SEMC); Valle Largo, 1♀ (UCDC); Valle Loboguerrera, 1♀ (SEMC)]; **Costa Rica** [Cartago Prov., 7♀ (SEMC); Golfitos, 1♀ (UCDC); Guanacaste Prov., 2♀ (SEMC); Limon Prov., 1♀ (SEMC); Monte Redunda, 1♀ (UCDC); PuertoViejo de Sarapiqui, 4♀ (CUIC); Puntarenas, 1♀ (SEMC); San Jose, 1♀ (UCDC), 1♀ (AMNH), 1♀ (SEMC); Wilson Hacienda, 1♀ (UCDC); locality not specified, 2♀ (MNHN), 1♀ (SEMC)]; **Ecuador** [Borbon, 1♀ (AMNH); Santo Domingo, 1♀ (AMNH) and 2♀ (MNHN); locality not specified, 2♀ (MNHN)]; **Nicaragua** [San Marcos, 1♀ (CUIC); **Panama** [Boquete, 3♀ (UMMZ); Canal Zone, 3♀ (SEMC), 1♀ (AMNH); Changuinola Dist., 3♀ (CUIC); Colon Prov., 5♀ (SEMC); Panama Prov., 3♀ (SEMC); Potrevillas, 3♀ (UCDC); Sta. Rita, 1♀ (UCDC)]; **Peru** [Lara 3♀ (UCDC); El Tucuco, 2♀ (UCDC); Merida, 2♀ (UCDC), 4♀ (AMNH), 1♀ (CUIC); PortachueloPass, 1♀ (CUIC); locality not specified, 2♀ (MNHN)]; country not specified [El Valle, 1♀ (CUIC); Sto. Domingo, 2♀ (MNHN)].

Epipona quadrituberculata: **Ecuador** ["Sarajacu" 1♀ [Holotype] (MSNG)].

Epipona tatua: **Bolivia** [Buenavista, 1♀ (CUIC)]; **Brazil** [Sinop, Mato Grosso State, 1♀ (UCDC); Porto Velho, Rondonia State, 1♀ (UCDC); locality not specified, 1♀ (AMNH)]; **British Guiana** [Bartica, 1♀ (CUIC)]; **French Guiana** [Kourou, 7♀ (SEMC)]; **Peru** [Huanuco, 1♀ (SEMC); Tingo Maria, 1♀ (AMNH); San Martin, 3♀ (AMNH); Ucayali River, 1♀ (AMNH)]; **Trinidad** [Nariva Swamp, 1♀ (AMNH)]; **Venezuela** [Caripito, 1 ♀ (AMNH)].